

THE MICROHABITATS OF WESTERN WOLF SPIDERS OF THE GENUS *Pardosa*

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Pardosa is the largest genus of the family Lycosidae in the western United States. Well over 50 species of this genus can be found in the mountain states while all other lycosids combined probably exceed that number only slightly. *Arctosa*, *Geolycosa*, *Tarentula* and *Lycosa* are present and possibly some of the other genera which have been established may be found. In central and eastern United States *Lycosa* seems to be the largest genus. Within *Pardosa* there are several species groups which have not been recognized subgenerically. Neither the genus nor the family have been monographed since Montgomery (1904) and Chamberlin (1908). Papers by Gertsch (1934), Barnes (1959), and Vogel (1964) have treated some of the groups of species but they have been mainly morphologically defined. Vogel (1964) characterizes the *distincta* group as "six closely related species. Their phyletic relationship is indicated by similar color pattern and genital morphology, and five of the six species occupy the same habitat". The taxonomy of the genus *Pardosa* is still confused and needs revision.

During the past ten years I have been studying the genus *Pardosa* of the western United States, particularly in the Jackson Hole and Grand Teton Range area of Wyoming, and trying to determine and characterize the microhabitat preferences of each of the species.

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Few ecological observations are in the literature. Tongiorgi (1966) presents a summary of what is known about the habitats of Italian pardosas. However, in many cases he had no data available about the major habitat and still less about the microhabitat in which a particular species occurs. Usually only the altitude range or type of habitat, such as meadow, or stream margin, is known. In defense of the small amount of microhabitat data, it must be said that microhabitats are not readily determined. Habitat preferences of these species are summarized here because of scarce information in the literature. The writer hopes this will call to the attention of other workers the specificity and importance of recording habitat preferences.

Wolf spiders of this genus are small (most species 5 - 8 mm), cursorial and nomadic. Each individual probably ranges only in a limited area. After emerging from the egg case the young climb onto the back of the female where they remain together for about 7-14 days. After leaving her back they become solitary carnivores for the rest of their lives except for the brief courtship period. Their microhabitat is the ground surface almost exclusively. They may run up onto blades of grass or on a floor of grass in those situations where grass does not stand erect but lies in great horizontal sheets. But otherwise, very few of them leave the ground to clamber upon shrubs, trees or other objects off of the ground. Some species, such as the European *Pardosa nigriceps*, seem to crawl up into the vegetation some of the time (Vlijm and Kessler-Geschiere, 1967). From extensive observations, it is apparent that only accidentally, or momentarily to avoid capture, do the western United States species move onto herbaceous or woody vegetation which is not lying horizontally, or nearly so, upon the ground. Sweeping of vegetation with a net has produced no specimens in thousands of sweeps in the western United States. In southeastern United States I have found immature lycosas fairly common at night upon vegetation. Neither adults nor juveniles are usually found on vegetation in the daytime.

The forest, meadow and similar habitats can be subdivided ecologically in such a way as to separate them into microhabitats on the basis of the following environmental factors.

I. The texture of the substratum may consist of 1) bare soil, 2) wood, such as fallen logs, twigs and branches, 3) rocks of various sizes, and 4) grass and/or other vegetation.

II. Moisture is another variable to which the spiders adjust. They prefer 1) very wet, 2) very dry, or 3) intermediate soil moisture conditions. Air moisture probably serves as another variable but it is even more difficult to evaluate and separate into categories than is soil moisture.

III. Another characteristic they adapt to is the temperature of the environment in which they live. Much of the difficulty in evaluating differences of habitats is due to the difficulty of determining what the particular habitat in which they occur is like with regard to soil and/or air moisture and temperature. In laboratory work it has been shown by Norgaard (1951) that some species do prefer different temperatures.

IV. Food is a factor since most of these spiders are of about the same size and hence competitors. The spiders also vary in size and hence in size of prey and probably species of prey.

V. The altitudinal distribution of habitats is limited. A number of spiders are confined to timberline and above in alpine tundra habitats, most range widely in intermediate altitudes from timberline down to a few thousand feet. Few species are limited to the lower altitudes although some, like those of the *P. sternalis* group, are more abundant at low altitudes. Individuals of species occurring at high altitudes will be found in greater numbers, between about 2400 - 3400 m, although more collecting will be needed before this can be definitely determined. The generalizations about altitudes apply roughly between 35° and 45°N lat in the western United States. South of 35°N lat the high altitude species disappear while lower altitude species replace those found to the north. North of about 50°N lat the low altitude species disappear or may be replaced by different species. High altitude species like *P. uintana*, *P. mackenziana*, *P. hetchi*, *P. anomala*, and *P. concinna* are found probably at lower altitudes north of 50°N lat. This is documented for *P. uintana* and *P. mackenziana*. It is hypothesized for the other species because they are high altitude

species but their occurrence at lower altitudes in the north is not documented. In the northeastern United States and adjoining Canada *P. uintana* and *P. mackenziana* are at low altitudes in coniferous forests. *Pardosa tristis* seems to be the only species in the west which is abundant from low altitudes to above 3400 m.

The following major habitats for spiders of the genus *Pardosa* can be identified:

1) *High altitude grasses, rocks and wood (fallen logs, bark or branches)* -- Temperature here is usually high when the sun is shining upon the ground while moisture is variable, depending upon the microhabitat, although generally low.

2) *Stream and lake margin boulders* (one cm up to one m or more in diameter, but round and water-worn) -- Temperature here is high when the sun is shining, but cool or even cold beneath the rocks. moisture is high beneath but much lower on top of the rocks.

3) *Talus rocks* -- Large to small, usually angular, boulders are formed in large masses, more commonly at higher altitudes, where cliffs disintegrate into a slope of rubble. In these talus slopes temperature and moisture vary from high to low depending upon where the spider may be. Here and in other habitats the spider moves about with the shift in day and night conditions, as well as with seasonal conditions. In a talus area a spider can adjust to temperature and/or humidity to utilize a wide range of these conditions.

4) *Streamside and lakeside grasses* -- This habitat forms a narrow strip in which moisture seems to be a major consideration. The *pardosa* may not always abide in the high moisture band next to the water but water is always available and the grass serves as a protection from the direct effect of the sun. Thus the spider can avoid heat, cold, dryness or moisture by moving to the area it prefers and still be in the same habitat. There is variation within this habitat in that long grasses produce a protected, variable and different habitat from the short grasses which screen out less of the effect of the sun and, typically, is a dry habitat. Open areas

where there is driftwood or other pieces of bark, logs or wood produce still drier conditions.

5) *Coniferous forests* -- Most forests of the West have very little surface vegetation, a minimum of sunlight and heat reach the forest floor and there is also probably a limited variety of food. Humidity here is generally high although as the forest dries out in late summer and fall the leaf litter layer becomes quite dry. In less dense forests, these spiders may differentiate in their distribution between moist and dry coniferous woods.

6) *Swampy moist meadows* -- These open treeless areas have populations of *Pardosa* not found elsewhere. Also some of the species of the above grassy habitats occur in this habitat.

7) *Treeless or open parkland areas* -- These areas of prairies and sagebrush are the driest and hottest of the habitats. The ground surface is much less inhabitable than in the other communities, and the variety of species much less, but a few species have become adapted to this habitat. True deserts (rainfall less than 20-25 cm) have no permanent wolf spider residents except where there are streams or springs.

Most species of *Pardosa* have fairly specific habit preferences while a few are found in a wide variety of habitats. Some live in ecotonal situations or are tolerant of more than one habitat. In some habitats several species have been found living together. In these situations the competitive exclusion principle is not operating at the time partly because prey is not in short supply.

SPIDER MICROHABITATS

Following is a species by species summary of the author's observations, and some observations from the literature, regarding each species, or species group, of the genus *Pardosa*. The species are listed by groups (probably subgenera). Included are data on species collected in the same localities as an indication of species which may be in competition with each other. Where there are no data on such interrelationships it is not an indication that there are none, but simply that only the one species has been collected in that habitat. These observations on species collected in the same

habitat are included to indicate that overlapping of habitat preferences occurs rather than to present a complete listing of possible species to be found in any particular type of habitat. Each species in areas of mixed habitat may not be found always in the precise microhabitat indicated. Finally, at the periphery of the range of a species it may occur in a slightly, or even greatly, different microhabitat.

I. The *distincta* group prefers the driest habitats of all species. Vogel (1964) has characterized the group in this way and all of my experience has corroborated this conclusion. These species are differentiated from one another mainly on their allopatric distribution although some species seem to have slightly different moisture requirements and some are syntopic as well as sympatric (Rivas 1964). This group is found in open plains, sagebrush and other non-forested areas except where forests adjoin open dry lands.

Pardosa distincta (Blackwall, 1846) and *Pardosa utahensis* Chamberlin, 1919, are low altitude species. I have collected them alone and together on occasion, but rarely with other species. Drier habitats are preferred by *P. utahensis* than by *P. distincta*. The species of this group have a low density in the areas where they occur, in the magnitude of $1/100 \text{ m}^2$.

II. The *glacialis* group is large in the west and difficult to characterize. However, it seems to be generally a moist meadow-inhabiting group. None are to be found in forests, although some occur in open meadows within a forest.

Pardosa anomala Gertsch, 1933, is one of the two main species completely restricted to high elevations in forested areas. *P. anomala* is found above about 3000 m in the Rockies and at lower altitudes farther north. It is found only in coniferous forest meadows, usually in areas moist from melting snow.

Pardosa coloradensis Banks, 1894, is found in low and mid-altitude meadows. Many individuals occur in moist meadows usually with bordering drier areas. This spider has been found in the Gros Ventre River Valley in both moist swales and irrigation ditches where sagebrush and dry meadows adjoining. A similar habitat was found east of Bridgeport, near Grand Coulee Dam, in

Washington. Here this species occurred in a nearly dry creek bed surrounded by grasslands. Although found as high as Togwotee Pass in the Tetons at over 3000 m, most of the records come from about 2000 m.

Pardosa concinna (Thorell, 1877) was recorded by Schmoller (1968) from timberline (about 3500 m) and above in Colorado. He characterizes it as being found in mesic alpine areas; subalpine forest edges on gravel and light mixed tundra vegetation such as species of *Geum* and *Kobresia*.

Pardosa fuscula (Thorell, 1875) is found in extremely wet areas with standing water, where the grass is often quite long (over 20 cm). I found it on the south side of Togwotee Pass in an exceptionally moist area, in the Blue Mountains of Washington (Target Meadows) in a high meadow with standing water surrounded by coniferous forest. Other locations are in a moist meadow in the forests of the Pioneer Mountains south of Wise River in Montana, and in a somewhat drier area along the grassy and rocky shore of Duck Lake east of Glacier National Park. In the Chicago area it inhabits tamarack bogs.

Pardosa johanseni Gertsch, 1933, does not seem to be common but has been found enough to indicate its habitat preferences. I have found this species in three widely-separated places in which sagebrush prairies have surrounded the collecting localities while the immediate site has been a moist pond or drying wet area of willows, sedges, herbs and mosses.

Pardosa ourayensis Gertsch, 1933, has been collected by Schmoller (1968, 1970) in pitfall traps in Colorado mainly at timberline, and above, in and on marsh grasses, among krumholz and in boulder fields with wet ground nearby. He characterized it as a hygric or marshy alpine species.

Pardosa tetonensis Gertsch, 1933, has been found with *P. distincta*, *P. altamontis*, *P. coloradensis* and *P. uncata*. Its general habitat is open, dry meadows. This species was found in Montana on the Yogo Peak Ridge east of Great Falls, in the Toll Mountain area southeast of Butte, in dry meadows bordering moist sedges and other spots in the Pioneer Mountains and near Dunraven Pass in Yellowstone National Park among sagebrush but where moisture

was in the vicinity. Therefore, this is a dry meadow species which has to be in an area near moisture.

Pardosa wasatchensis Gertsch, 1933, occurs in tall grass, in an aspen 'swamp', and in a wet timothy field below Uhl Hill in the Jackson Hole area. These data place it as a moist meadow form. It is a rare species and further characterization of its microhabitat is needed.

III. The *lapidicina* group is found among boulders and gravel beside streams and lakes at all low and mid altitudes in the west, and east.

The distribution of *Pardosa steva* Lowrie and Gertsch, 1955, and *Pardosa sierra* Banks, 1898, is geographical rather than ecological (they are mainly allopatric). The author has collected along many boulder-strewn stream beds in the West and finds many areas lacking spiders. Other areas contain more than just *lapidicina* group species. The boulders nearly level with the stream but not imbedded in the gravel will typically have *lapidicina* group members while the borders of the boulder piles will have other species from grass and adjacent microhabitats. These species are found usually at the lower to median altitudes, although they may occur along streams at elevations up to 2200 m.

IV. The *mackenziana* group consists of species occurring on the ground within coniferous forests. Two species occur at timberline or above, but adjoining forests. The sympatric species may be in slightly different parts of the forests based on moisture differences. Characteristic of this group is its low densities.

P. mackenziana (Keyserling, 1877) and *P. uintana* Gertsch, 1933, are both geographically and ecologically separated from *uncata* and *P. dorsalis*. Geographically they are widespread throughout Canada and northern United States and occur sympatrically and often syntopically. Schmoller (1968) indicated that in Colorado they are found at high altitudes (over 2700 m), and they may live in separate microhabitats. In a series of pitfall traps in a *Picea-Abies* stand he recorded 70 *P. uintana* but no *P. mackenziana* whereas he found 28 *P. mackenziana* but no *P. uintana* in a *Pinus contorta* stand. In the Tetons I have found only *P. uintana* above 3000 m among the high altitude conifers. In

Canada and Alaska these two species are common at sea level but always in coniferous forests.

P. hetchi Chamberlin and Ivie, 1942, is restricted to tundra areas above timberline. It has been found only in Colorado, Washington and California but in all areas it was well above timberline (usually 3300 m or higher). Whether it is restricted to these high altitudes due to temperature, moisture or substratal and prey relationships is unknown; however, its microhabitat preference among alpine tundra rocks and vegetation above timberline seems clear.

The habitat preferences of *P. uncata* (Thorell, 1877) and *P. dorsalis* Banks, 1894, are difficult to characterize but *P. dorsalis* seems to prefer drier woods than *P. uncata*. *P. uncata* is widespread from east to west in northern United States and southern Canada while *P. dorsalis* is restricted to northwestern United States and adjacent Canada. These species are found at lower altitudes than the other *mackenziana* group species. *P. uncata* may be found under and on bark of fallen trees on the ground but is always found distinctly within the forest while *P. dorsalis* is at times to be found on trails in open meadows within the forests. Pitfall trapping would aid in determining more specifically the microhabitats of these species.

V. The *sternalis* group occurs in short grass where the spiders can emerge onto rocks and dead branches. These are not meadow species because they also occur beside streams and within woods.

Pardosa altamontis Chamberlin and Ivie, 1946, lives at low to mid-altitudes although specimens have been collected from as high as 2700 m in the Tetons at Delta Lake. *P. ramulosa* (McCook, 1874) individuals in the Los Angeles area occur at altitudes less than 1000 m. One collection was made, however, at about 3000 m in the Sierras of California (Vogel, 1970). Likewise, *P. vancouveri* Emerton, 1917, seems to be restricted to low altitudes. The habitat is typically short grass up to 5-10 cm. They crawl in open bare spots and on fallen branches and twigs. They will crawl up onto any solid object such as rocks, housebricks, branches or logs to sun themselves, especially the females when incubating egg sacs. *P. ramulosa* is a common inhabitant of the margins of mowed lawns in the Los Angeles area as is the case with *P. vancouveri* in

the Astoria, Washington locality. This group is abundant wherever found. Borders of lawns where there is a wall have populations of 5-10/100 cm², whereas the main lawn will be nearly devoid of adults and young are very sparse.

VI. The *groelandica* group apparently consists of only *P. tristis* in the west. Its taxonomy is not clear.

Pardosa tristis (Thorell, 1877) is widely distributed geographically, altitudinally, and ecologically. It is the largest species of the genus and may therefore be less dependent upon temperature and humidity variation as well as less competitive with smaller syntopic species. It is common in the vicinity of water. It has been found from sea level to altitudes nearing 3000 m. I have collected it within a short distance of a stream or lake except at the highest altitudes and often it is running among rocks in a stream as well as in the soggy ground of nearby marshy areas. It is not only widespread in the West and at almost all altitudes, but is probably the most common species of *Pardosa* if one were to collect only in moist areas. I have not found it in habitats which are very dry, in the middle of talus rocks, or on bare ground. Schmoller (1970) indicated that in the higher altitudes in Colorado it occurred in rocky, alpine dry habitats. Since it can, and possibly does, feed exclusively upon fairly large insects, it would not compete with most members of the genus. I have collected it more commonly with *P. uncata*, a forest species, less commonly with *P. xerampelina*, *P. wyuta*, and *P. fuscula*. In addition, I have collected it once each with 5 other species. In summary, the spider is typically found where the habitat is fairly moist although it will wander into some bordering dry open areas. It may be in openings in woods, along the edge of woods, or on driftwood but only where there is grass nearby.

VII. This species is a member of the genus *Acantholycosa* or at least belongs in a group by itself. From European and American records I have examined, it is certain that this is a talus rock species and possibly genus.

Pardosa solitudo Levi and Levi, 1951, was discovered "running between stones in meadow" on the southeast shore of Lake Solitude in Grand Teton National Park. Further collecting has narrowed this habitat down to talus slopes. In any talus area

several other species of pardosas may be found around the edges where grasses or fallen wood produce an ecotone. But, in the inner part of an extensive talus slope of rocks, the small dark gray spider is usually *P. solituda*. Altitude is probably unimportant except at the higher elevations where weather conditions may become too severe for this species. I have found it in talus in the Pioneer Mountains near Butte, Montana, and in Glacier National Park. It is still a "rare" species, partly because it is extremely difficult to catch due to inaccessibility in talus rocks and its rapidity of movement.

VIII. The following species are either alone in the group to which they belong, or the group is not well identified.

I have collected *Pardosa californica* Keyserling, 1887, in some of the lawns of the Los Angeles area but it is most common along streams. David W. Hagstrum (personal communication) has found high densities of this species in a moist coniferous forest meadow near Lake Fulmor above 1650 m on Mount San Jacinto in Southern California.

Pardosa moesta Banks, 1892, occurs in moist areas around Two Ocean Lake in the Tetons and Bowman Lake in Glacier National Park, in a meadow of long grass on the Olympic Peninsula, and in long grass near Mount Vernon, Washington. It was also along the Touchet River, in Montana in tall sedges beside Saint Mary's Canal northeast of Glacier National Park and in Wyoming beside Lafferty Creek in the Gros Ventre River Valley. All these areas were moist, with tangles of long grasses 50-100 cm long.

Pardosa tesquorum (Odenwall, 1901) has been found in association with *P. distincta* at one place east of Glacier National Park in tall grass and with *P. tristis* in the same general area. In the Tetons it has been found in six localities: along the Gros Ventre River, Pacific Creek among gravel, boulders and grass, in long grass beside the Snake River, above Cascade Creek, around Marion Lake and the shores of Two Ocean Lake. All but one of these is about 2000 m.

Pardosa wyuta Gertsch, 1934, has been found with 8 other species at various places. It was collected mainly with *P. tristis* and *P. altamontis*, and secondarily with *P. uncata* and *P. fuscula*. In the Tetons it has been found only in a lakeside, grassy meadow

beside Arrowhead Pool at 2750 m. In Glacier National Park it was in grassy areas beside Iceberg Lake at 3050 m. It seems to prefer altitudes around 2000 m. In the Wallowa Mountains of Oregon it is in moist, as well as dry, meadows bordering streams. In the northern mountains of Washington, it occurs in the forests among rocks beside the Nooksack River. In Mount Rainier National Park it occurs in forests beside the White River, and in long grass and short herbs beside Clear and Rimrock Lakes, outside the Park to the Southeast.

Pardosa xerampelina (Keyserling, 1877) has been collected most commonly along the Death Canyon stream at 2000 to 3000 m in the Tetons. It is found there in grass and driftwood immediately bordering the streams where it has access to both dryness on top of the driftwood and the moisture of the stream and the grass below. Generally it is a forest form, always occurring beside a stream and particularly in open clearings. It has been collected with *P. tristis* and *P. uncata* on one occasion each.

REMARKS

Data which I have collected in the Chicago area (Michigan, Indiana, Illinois, Wisconsin) indicates that those species found there as well as in the west, show much the same habitat preferences. *P. distincta*, *P. fuscula*, *P. lapidicina*, *P. mackenziana*, *P. moesta*, *P. tristis*, *P. uncata* and *P. xerampelina* have all been found and fit into the habitat descriptions except that they are all at low altitudes. Where habitat data has been available the same has been true of Canadian specimens of *P. coloradensis*, *P. concinna*, *P. distincta*, *P. lapidicina*, *P. mackenziana*, *P. moesta*, *P. tristis* (or *groenlandica*), *P. uintana*, *P. uncata*, and *P. xerampelina* sent to me by Dondale and Buckle.

Other species could be mentioned for which isolated data on habitats are available but I judge it best at this time to go no further with these habitat preferences because the data on most of the other species are too meagre. Pitfall trapping would be a helpful adjunct to field observations in areas where two or more species seem to coexist, in order to determine the degree of overlap. Some laboratory work with the species to note temperature and humidity preferences may be worthwhile although at present humidity preference work shows less promise than length of

survival time in a dry atmosphere. Work in all these areas is continuing and information would be welcome from anyone who has precise ecological habitat data and species records. In addition authors are encouraged to include microhabitat data on all spiders when describing species characteristics.

TABLE I. Summary of the microhabitats of the spider genus *Pardosa*.

	Wet Habitats	Habitats with Variable Moisture Conditions	Dry Habitats
Variable Altitudes		<i>californica</i> , <i>wyuta</i> , <i>xerampelina</i> dry to moist grasses and downed wood, often beside streams	<i>distincta</i> group dry open lands at low and mid altitudes
	<i>tesquorum</i> , <i>moesta</i> long grass moist to wet	<i>lapidicina</i> group low and mid altitudes among boulders and gravel beside streams and lakes	
		<i>sternalis</i> group moist to dry, short to medium length grasses and downed wood and rocks	
	<i>fuscula</i> (<i>glacialis</i> group) only in very wet, swampy habitats	<i>glacialis</i> group meadow habitats some dry (<i>tetonensis</i> & <i>johanseni</i>) but most in moist to very wet habitats	<i>solitudo</i> in talus rocks up to high altitudes
		<i>mackenziana</i> group coniferous forest - mainly moist habitats	
		<i>tristis</i> all altitudes all moisture conditions	
High Altitudes Below Timberline		<i>uintana</i> and <i>mackenziana</i> <i>mackenziana</i> group coniferous forests at higher altitudes in south and west parts of range lower altitudes in north and east	
		<i>anomala</i> (<i>glacialis</i> group) moist meadows within coniferous forests	
Above Timberline	<i>ourayensis</i> (<i>glacialis</i> group) hygric alpine	<i>concinna</i> (<i>glacialis</i> group) in tundra turf and forest edge	<i>hetchi</i> (<i>mackenziana</i> group) in drier habitats

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ABSTRACT: The microhabitat preferences of species of the genus *Pardosa* of the family Lycosidae (wolf spiders) found in the western United States are summarized. In the western United States these spiders are almost completely restricted to the ground surface and objects upon the ground. Extensive sweeping has not yielded any specimens in the vegetation. Habitats and spiders mainly associated with them, where identified, are the following: 1) grasses, rocks and downed wood at high altitudes, 2) boulders and pebbles beside lakes and streams (*lapidicina* group), 3) rocks of talus slopes (*P. solituda*), 4) grasses beside lakes and streams with separate microhabitats of long grasses, short grasses and rocks and driftwood, 5) coniferous forest floor (*mackenziana* group), 6) moist to wet meadows (*glacialis* group), 7) dry sagebrush and other open prairie and dry forested areas (*distincta* group).